same species from Burma should be the three wings you send me, which you say you found on the ground."—E. B. P.]

15. Guy A. K. Marshall's Indirect Evidence of the Attacks upon Butterflies. (E. B. P.)

At the meeting of the Entomological Society held on August 1, 1883, Professor Meldola communicated some observations made by Dr. Fritz Müller in Brazil (Proc. Ent. Soc. Lond., p. xxiii), together with specimens of distasteful conspicuous butterflies with wings notched or otherwise injured apparently by birds. Dr. Fritz Müller's well-known theory, which accounts for synaposematic resemblances, implies that even distasteful butterflies are experimentally attacked by young enemies. That such attacks are made had been doubted, and Professor Meldola therefore wrote to Dr. Müller asking him to collect observations upon the point. A specimen of *Heliconius cucrate* sent by him to Professor Meldola was described (Ann. Mag. Nat. Hist., Dec. 1882, p. 419) as having a symmetrical, jagged notch on both fore-wings; and on Aug. 1, 1883, Professor Meldola exhibited examples of thirty-six notched and shorn specimens of *Acræa* [*Actinote*] *thalia*, obtained in one week by the great German naturalist. These examples and the *Heliconius* have been presented by Professor Meldola to the Hope Department, where they may be seen beside numerous similar specimens from very different parts of the world, including those figured on the accompanying Plates IX, X, and XI. Similar observations upon Bornean butterflies, including four *Danainæ*, have been published by S. B. J. Skertchley (Ann. Mag. Nat. Hist. (6) iii, 1889, pp. 477–485), while W. L. Distant has described unsymmetrical injuries, apparently caused by a bird, in the wings of *Limnas chrysippus* ("Naturalist in Transvaal," 1889, p. 65). I noticed the same thing (1888) in many specimens of *Colias edusa* captured in Madeira ("Colours of Animals," London, 1890, p. 206; see also Roland Trimen's Presidential Address to the Entomological Society of London, Jan. 19, 1898, where many of these and other records are collected and commented upon).

It seemed of importance to obtain this kind of evidence from as many parts of the world as possible and on a large scale. I therefore asked Mr. Marshall if he would kindly

look out for specimens of butterflies bearing injuries which were probably caused by birds or other enemies. The results, as in every other instance in which I have asked for his help, far exceeded my most sanguine hopes. He sent me the fine series of injured specimens represented on Plates IX, X, and XI.

Looking at the species represented in this collection one is at once struck with the repetition of the very forms which have been seen to be attacked by birds (see pp. 357 to 359). Thus *Atella phalantha*, once *seen* to be mutilated by a bird (p. 357), is represented by no less than five injured specimens (Plate IX, figs. 9 and 12; Plate X, figs. 2, 4, and 5). And nearly every other species observed to be attacked or found in the stomach of a bird is also represented, often by two or more examples, in the three accompanying plates.

The presence of specially-protected forms, *Danainæ* and *Acræinæ*, is as conspicuous as in the observations made in other parts of the world; but new and interesting light is thrown upon the problem by the examination of these specimens and comparison with those of other more palatable groups. A large proportion of the former (Plate IX, figs. 1, 5, 7, 10, 11) are far more extensively mutilated than any but exceptional instances among the latter, and remarking the peculiar toughness, flexibility, and power of recovery in the wings of *Danainæ* and *Acræinæ*, we are driven to the probable conclusion that the results are in many cases those of experimental trials by young enemies and heroic attempts on the part of extremely hungry enemies, rather than unavailing efforts at the capture of palatable prey. The futile attempts of hungry animals, accompanied by extensive mutilation of unpalatable insects, are well known in confinement (Proc. Zool. Soc., 1887, p. 191), and Mr. Marshall has made observations of the same kind upon insect enemies in the wild state (see pp. 318, 358, 359).

The conclusion that butterflies may be pursued when specially easy to catch, suggested by the observations on April 26, 1899 (p. 358), is somewhat confirmed by the curious fact that all the five examples of *Limnas chrysippus* are females (Plate IX, figs. 1, 5, 10, and 11; Plate X, fig. 1).

Of the conspicuous wet phases of the seasonally dimorphic *Precis* only a single example is present (Plate IX, fig. 24),

whereas six examples of the cryptic dry phase are included in the series (Plate IX, figs. 15, 19, and 23; Plate XI, figs. 1, 2, and 4). These facts may possibly lend some support to the suggested interpretation of these remarkable changes (see pp. 431 to 442).

Some naturalists may be inclined to interpret the injuries represented on Plates IX, X, and XI as the ordinary results of age and wear, or the accidental contact with thorns or twigs. Such an explanation is not consistent with the fact that the great majority of the specimens are in other respects fresh and unworn, and the margins of the wings not frayed as they become in individuals which have been long upon the wing. Again, the very high proportion of the injuries inflicted at the anal angle and along the hind margin of the hind-wing is inconsistent with any such interpretation. The part of the wing surface which is certain to come most in contact with foreign objects is the apical angle of the fore-wing, next, the costal and hind margins of the fore-wing, last of all the border of the hind-wing which is behind, and, as the insect finds its way through an interlacing meshwork of twigs and leaves, is defended by the greater width and powerful costa of the fore-wings. It is true that the apex of one or both fore-wings is not uncommonly snipped off, several examples being represented on Plate IX, and in the four lowest figures on Plate XI, but the great majority of the specimens captured by Mr. Marshall will be found to be injured in the hind-wing. And of those snipped or notched in the fore-wing, some exhibit symmetrical injuries which clearly suggest that the insect was seized with the wings together, probably at rest. Figs. 12 and 17 on Plate IX are good examples. Equally symmetrical injuries are also common on the hind-wings, either taking the form of a snip which suggests the very shape of a bird's bill (*e. g.* Figs. 4, 30, 31, 33 on Plate X), or one in which both anal angles or even a large part of both hind-wings are shorn completely off (*e. g.* Figs. 2 and 28 on Plate X; Figs. 8, 9, 18 and 20 on Plate XI).

In one very interesting example of *Vanessa atalanta* from N. Devon, presented by Dr. F. A. Dixey to the Hope Department, there is only one possible position in which the injury could have been inflicted, viz. the position shown in Fig. 31, Plate X, for in that position alone can the snip *in all four wings* be made to coincide. Furthermore, the position is that of complete repose, when the

white patch on the costal border of the under-side of one hind-wing, wrapping round the front of the costa of the fore-wing, meets the corresponding patch on the opposite side, and is distinctly seen from the front. The specimen captured by Mr. A. H. Hamm, represented in the adjacent Fig. 33, was probably seized soon after it had alighted, when the wings were held in the manner indicated in the figure, and before they were lowered between the hind-wings in the attitude of repose. Or it is possible that this specimen was seized during flight at the moment when the wings came together.

The theory of probability prevents the interpretation of any but very rare symmetrical notches, except on the supposition that the wings were together at the time of the injury, and when the condition of the specimen is fresh and the notch possesses a definite and similar shape, fitting that upon the opposite side, there can be no hesitation in inferring the attack of an enemy.

Turning to unilateral injuries, of which many examples will be found in Plates IX, X, and XI, Mr. Marshall is of opinion that they are the strongest evidence of the attacks of birds because they were almost certainly inflicted while the insect was upon the wing. Perfectly fresh specimens with such injuries of a very pronounced type are shown on Plate IX, figs. 15, 19, and 23; Plate X, figs. 1, 3, 5, 19, 25, 29, etc.; Plate XI, figs. 4, 6, 7, 11, etc. It is true that a butterfly settled upon a flower with outspread wings might be seized by one side; but insects in that position are on the alert, and many butterflies when slightly disturbed will shut their wings with a snap when they do not take flight.

Looking at the injuries as a whole it is seen that the great majority are inflicted at the anal angle and adjacent hind margin of the hind-wing, a considerable number at or near the apical angle of the fore-wing, and comparatively few between these points, at or near the inner angles of the wings. I was at first greatly struck by the comparative rarity of injuries in the last position, but in a later consignment Mr. Marshall forwarded many excellent examples, referred to in the following paragraph:—

"*Salisbury, Sept.* 27, 1901.—It was curious that just after getting a letter from you, pointing out the greater rarity of mutilation at the inner angles, I came across quite a succession of excellent examples of this form. The

Teracolus omphale is of special interest, as I think the attack can only have been made by a bird. The same applies to the *Nyctemera*, for this insect invariably conceals its hind-wings when settled, dropping immediately into this position as it alights. I have occasionally observed that it holds its wings over its back for a very short time before closing them. I think the damage to the hind-wings must be the result of two separate snaps from a bird while the moth was on the wing."

The specimen of *Teracolus omphale* was accidentally omitted from the illustrations, but the *Nyctemera* is shown on Plate X, fig. 8, and three of the best examples of injury at an inner angle on Plates IX, figs. 15, 19, and 23.

If it be granted that the injuries shown on Plates IX, X, and XI are chiefly if not entirely due to enemies, the question as to the kind of enemy remains to be settled. The only probable foes are birds, reptiles, especially lizards, and mantides. It is therefore of importance to show that injuries entirely similar in character to those upon Mr. Marshall's South African captures, are also found on butterflies from parts of the Holarctic Belt where mantides do not exist and the attacks of lizards amount to so little that they may be safely neglected.

I have therefore included (on Plate X, figs. 26 and 28 to 33) the representation of a few butterflies with snipped wings from the Northern United States, Switzerland, and England. These are only a selection from a much larger amount of material of this kind in the Hope Department, but sufficient to show that the character of the injuries in the northern land belt is the same as that of those far south of the Equator, and in a country where lizards and mantides are very important foes.

Much however may be determined by the character of the injury and the habits of the butterflies. Such an injury as that shown on Plate X, fig. 4, for example, is hardly likely to have been caused by anything but the beak of a bird. When a mantis seizes a butterfly with its raptorial legs the wings are instantly crumpled and at the same time torn and scratched with the thorn-like spines. Only two or three specimens out of the 82 here figured bear any such traces, viz. Plate I, figs. 7, 11, and Plate XI, fig. 5, and in these cases the interpretation is very far from certain. With regard to lizards, butterflies which settle on low flowers, and especially those which alight

on the ground and rocks, are very liable to be attacked, but in South Africa at least, species which haunt bushes and trees and fly high are not likely to fall a prey to lizards, and birds are the only probable enemies when no traces have been left by a mantis. In the description of Plates IX, X, and XI, a brief account of the habits of each South African species is given by Mr. Marshall together with the conclusion which appears to be justified.

A very interesting general conclusion emerges after this consideration and comparison of all the specimens here figured, viz. the bionomic meaning of important elements in pattern, and important structural developments of the wings of Lepidoptera. On Plate IX we see evidence that injury at the apical angle of one or both fore-wings is fairly common. Now this angle is very remote from the vital parts, and no great harm to the butterfly is done by such injury. And this is a part of the wing which is constantly rendered specially conspicuous below as well as above by apical and sub-apical white spots and bars, black tips, patches of bright colour, and by eye-spots (Plate IX, figs. 1, 3, 15, 16, 20, 21, 22, 23, 25; Plate X, figs. 3, 8, 19, 25, 28, 32, 33; Plate XI, figs. 4, 21, 22, 23, 24). In the four lowest figures on Plate XI the conspicuous apical marking has been injured and, in three cases out of four, partially or entirely shorn off on one side. This interpretation of the meaning of the apical colour-patches was suggested by Mr. Marshall in sending these very specimens, and he alluded to two out of the three butterflies figured on Plate XI, figs. 21–23, in the following passage:—

"*Salisbury, June* 20, 1899.—I would suggest that these bright patches of colour [in the orange- and purple-tipped *Teracoli*], which were doubtless first developed by sexual selection, have been of further use in diverting attack from the vital parts, and this may perhaps explain their almost universal transmission to the female sex. I have sent you two good examples supporting this view, in that the orange tip of one wing has been snipped off, presumably by a bird. It should however be noted that the *purple* tips are very inconspicuous in flight, and perhaps this might account for the markedly-swifter flight of those species which possess them, as they will have thus lost a useful protection through the action of sexual selection, and have compensated it by increased swiftness." *

* Dr. F. A. Dixey points out to me that it is in favour of this

Notches close to and sometimes involving the same kind of markings are to be seen on Plate IX, figs. 1, 3, 5, 10, 16, 19, and 21.

We can thus understand the conspicuous apical markings of the fore-wings of butterflies, together with the common prolongation of the apex of the wing, as directive marks which tend to divert the attention of an enemy from more vital parts.

The comparison of Figs. 31 and 33 on Plate X will show a common method in the use of this marking on the under-side. It is exposed for a few seconds after the butterfly alights (Fig. 33), and then hidden by lowering the fore-wings between the hind (Fig. 31). The meaning is no doubt that which is suggested on pp. 440, 441, where it is however applied to the case of those sub-apical eye-spots on the under-side (Plate X, figs. 28 and 32) which are exposed and then hidden in a similar manner.

Since the above sentence was written I have consulted my assistants, Mr. W. Holland and Mr. A. H. Hamm, who have had great experience in the ways of British Lepidoptera, and they both agree with me that our species of *Satyrinæ* with special sub-apical eye-spots on the under-side of the fore-wing are apt to expose these marks for a few seconds after alighting, and then swiftly cover them by lowering the fore-wings between the hind. The "Grayling," *Satyrus semele*, is particularly noticeable in this respect, as all three of us have often observed; but the movement is well seen in our other species with similarly-placed eye-spots.* This characteristic movement considered in relation to Mr. Marshall's injured specimens, and to the experiment with a lizard mentioned on pp. 440–1, and a kestrel on p. 341, places the hypothesis advanced on the former pages in a satisfactory position.

But the interpretation of markings and structures at or

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interpretation that the *females* of the species with purple-tipped males are themselves often orange-tipped.

* Dr. Dixey has specially observed this movement in *semele*. He states that *Epinephele janira*, on the other hand, usually shows the eye-spot when resting by day, although it quite conceals it when settling down in the evening: while a ♀ *E. tithonus*, settled on a bramble-leaf in sunshine, exposed the ocellus, but concealed it when a cloud came over the sun, again uncovering it when the cloud passed. Dr. Dixey's notes were made at the time of the observations at Morthoe, North Devon, in 1897–8.

near the anal angle of the hind-wing is even more convincing, inasmuch as both markings and structures are far more specialized and examples of their injury much commoner. Plate X is entirely occupied with the representation of such injuries in species which are without special directive marks and structures at this region of the hind-wing, while Plate XI, with the exception of the four lowest figures (21 to 24) and figure 4, is devoted to the illustration of injuries received at the very spot which has been rendered specially conspicuous. In fact, on Plate IX we have evidence that the attacks of enemies are common at the apical angle of the fore-wing, and on this Plate as well as in the four lowest figures of Plate XI the special directive marks developed at this specially-exposed area are seen to be shorn off or in some way injured; while on Plate X we have the same kind of evidence of still more frequent attack at the anal angle of the hind-wing, together with, on Plate XI, the evidence that this general tendency on the part of the enemy is encouraged by the development of directive features of all kinds, which are shown to be successful in that they have been attacked. We see on Plate XI the prolonged "tails" of the hind-wings of *Precis* shorn off (Fig. 1), together with the large eye-spot marking the same region in *Papilio demodocus* (Figs. 8 and 9), the two "tails" of *Charaxes* (Figs. 5, 10, 13, 14, 15, 20), the slender single "tail" with its accompanying single or double eye-spot of some *Lycænidæ* (Figs. 6, 11, 16, 17), the conspicuous lobes combined with one or two "tails" and bright spots, sometimes in the form of eye-spots, of other *Lycænidæ* (Figs. 3, 7, 12, 18, 19).

Many beautifully "tailed" forms occur among the *Nymphalinæ* of tropical America, such as *Protogonius*, *Anæa*, etc., and the commonly developed "tails" of Papilios are probably to be explained in the same manner. When a "tail" is produced at the anal angle of the hind-wing in relation to a dead-leaf-like under-side, the mid-rib-like stripe is developed in relation to the apparent leaf stalk, as is seen in Plate XIII, figs. 4a, 4b, 6, 7, and 8. On the other hand, Fig. 1 on Plate XI shows well that such "tails" may also act as advantageous directive structures.

The resemblance of the marks and structures at the anal angle of the hind-wing under-side in many *Lycænidæ* to a head with antennæ and eyes has been independently noticed by many observers. The movements of the hind-

wings by which the "tails," the apparent antennæ, are made continually to pass and repass each other, add very greatly to this resemblance. The head-like appearance, first observed by Dr. Arnold in *Thecla iarbas* and confirmed in other species by Dr. Forsström, is quoted by Kirby and Spence (People's Edition, 1867, p. 423): it was independently observed by Mr. R. C. L. Perkins ("Colours of Animals," London, 1890, p. 208) in *Thecla W-album*, and this keen naturalist obtained confirmatory evidence in the case of the English *Thecla*, similar to that shown upon Plate XI. My friend Dr. Richard Evans of the Museum at Georgetown, British Guiana, independently observed the same thing in Siam, when taking part in the Skeat Expedition. My friend Professor Wyndham R. Dunstan, F.R.S., sending me a pair of *Deudorix antalus* bred from larvæ which are destructive to the pods of "*Inga dulcis*" at Manashi, near Cairo, wrote (July 4, 1900) that his friend Mr. E. A. Floyer who sent the insects "remarks that the butterfly has markings on its tail which resemble the head. He considers this protective, as a bird is uncertain which is the head and which is the tail, and the insect often escapes by going off in the unexpected direction." My friend Mr. Champion B. Russell, who presented to the Hope Department the beautifully mutilated specimen of *Spindasis natalensis* represented on Plate XI, fig. 3, also independently recognized the same resemblance (1900), and thought that the lobes with their two tails passing and repassing each other looked like jaws opening and shutting. I asked Mr. Marshall's opinion on this subject and received the following reply:—

"*Salisbury, June* 11, 1901.—Mr. Russell's observations on the tails of *Lycænidæ* are, as you say, of considerable value as coming from an entirely independent source, but I must confess that I am not inclined to believe that the anal appendages in the wings of butterflies have been modified in imitation of particular organs, for I fail to see how this could be effected by ordinary selection. And I think a valid argument against such an idea is the great diversity of form shown by these appendages, not only among the *Lycænidæ* but other families as well. It seems safer to regard these curious lobes and tails as having been developed by natural selection for the purpose of attracting attention to that part, and that the particular form they take is due to congenital variations which we cannot

at present explain. As a matter of fact there seem to be really very few "blues" in which the tails bear any real resemblance to antennæ. Again, so far as the special explanation of jaws is concerned it seems to me that this would rather prompt a bird or lizard to attack the insect at the other end, which would be fatal. In some cases there appears to be a possibility of explaining the particular shape of a tail; for example, in *Charaxes* the general rule is two thin tails on each wing, and we can understand that this would not be suitable for the leaf-like under-side of *C. varanes*, which has consequently developed a single thick tail which is more in keeping with its style of coloration. Again, the thick twisted tail of *Myrina* greatly enhances its general resemblance to a bit of shrivelled fig-leaf, and so forth."

I think, however, that it is probable that such resemblance as there is to a head, in certain species of *Lycænidæ* may be of value and may have been produced by direct selective action, and I would specially draw attention to Mr. Floyer's suggestion (p. 374) that the butterfly may dart off in a direction which the head-like appearance has caused to be unexpected by an enemy. Many years ago my friend Dr. A. C. Haddon, F.R.S., showed me a specimen of a little yellow fish, about 1¼ inches long, which he had observed and captured among coral, Aug. 11, 1888, at Thursday Island, Torres Straits. The head was crossed by a dark, white-bordered, vertical, somewhat curved band, which included the eye and tended to conceal it. At the root of the tail was a very conspicuous eye-like mark. The fish had the habit of often swimming for a little distance very slowly tail first, but if disturbed it would dart off with great rapidity in the opposite direction, viz. head first. That so similar an adaptation should be met with in such a very different part of the animal kingdom affords considerable indirect support to the interpretation of these Lycænid marks and structures, at which so many naturalists have independently arrived. Dr. Haddon kindly permits me to make use of his interesting observation, which has not been hitherto recorded. Mr. G. A. Boulenger, F.R.S., informs me that the fish is *Chætodon plebeius*.